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ABSTRACT
The Toarcian ammonite genus *Porpoceras* Buckman, 1911 is a cosmopolitan taxon with an uncertain stratigraphic range. The oldest known occurrence of the genus was reported from the Falciferum Subzone (Early Toarcian) in Morocco, although based on a unique specimen whose taxonomic assignment to the genus *Porpoceras* remains doubtful. The youngest occurrence was a simple mention of *Porpoceras* sp. from the Variabilis Subzone (Middle Toarcian) of the Thouars area (Western France), but it was later regarded as doubtful because no specimen was figured. We here provide the first robust evidence for the youngest known occurrence of the genus *Porpoceras*, from the Variabilis Subzone of the Thouars area. The known revised stratigraphic range of the genus therefore extends from the Falciferum Subzone to the Variabilis Subzone. In turn, the genus *Porpoceras* likely went extinct in the Illustris Subzone together with the genera *Catacoeloceras* Buckman, 1923 and *Mucrodactylites* Buckman, 1928, coinciding with the drastic loss of diversity observed between the Bifrons and Variabilis Zones in northwestern Europe (also known as the Bifrons-Variabilis extinction). Finally, in the light of our new data and of previous reports, the genus *Porpoceras* is not a foolproof biostratigraphic marker of the NW European Bifrons Horizon, although it remains an important taxon for identifying this biostratigraphic unit.

KEY WORDS
ammonite,
Lower Jurassic,
Dactylioceratidae,
Porpoceras,
Toarcian,
biostratigraphy.

RÉSUMÉ
Révision de l'étendue stratigraphique du genre d'ammonite Toarcien Porpoceras *Buckman, 1911.*
Le genre d'ammonite Toarcien *Porpoceras* Buckman, 1911 est un taxon cosmopolite présentant une étendue stratigraphique incertaine. La plus ancienne occurrence connue du genre provient de la sous-zone à Falciferum (Toarcien inférieur) du Maroc, cependant sur la base d'un spécimen unique dont l'appartenance au genre *Porpoceras* reste douteuse. L'occurrence la plus récente était une

simple mention de *Porpoceras* sp. dans la sous-zone à Variabilis (Toarcien moyen) de la région de Thouars (ouest de la France). Du fait de l'absence de spécimen figuré, cette mention fût considérée comme douteuse. Nous apportons dans ce travail la première preuve de la plus récente occurrence du genre *Porpoceras* dans la sous-zone à Variabilis de la région de Thouars. L'étendue stratigraphique connue à ce jour du genre s'étend donc de la sous-zone à Falciferum à la sous-zone à Variabilis. En conséquence, le genre *Porpoceras* s'est probablement éteint dans la sous-zone à *Illustris*, en même temps que les genres *Catacoeloceras* Buckman, 1923 et *Mucrodactylites* Buckman, 1928, coïncidant avec la perte drastique de diversité observée entre les zones à Bifrons et Variabilis dans la province nord-ouest européenne. Enfin, sur la base de nos nouvelles données et de précédents travaux, il apparaît que le genre *Porpoceras* n'est pas un marqueur biostratigraphique infaillible de l'horizon à Bifrons dans la province nord-ouest européenne. Ce genre reste néanmoins un important taxon pour identifier cet horizon.

MOTS CLÉS
ammonite,
Jurassique inférieur,
Dactylioceratidae,
Porpoceras,
Toarcien,
biostratigraphie.

INTRODUCTION

Among Toarcian ammonites, the Dactylioceratinae Hyatt, 1867 is undoubtedly the subfamily containing the highest number of named taxa, with 43 genera and 230 species reported in the literature. Rulleau *et al.* (2013) recently revised the taxonomy and systematics of this subfamily and retained 170 valid species belonging to 22 genera or subgenera (see also the significant work of Jiménez & Rivas 1991). Among them stands the genus *Porpoceras* Buckman, 1911 that is one of the most renowned genera of the subfamily, because of its cosmopolitan distribution. This genus, commonly regarded as an excellent marker of the Middle Toarcian Bifrons Horizon in the NW European realm (Rulleau *et al.* 2001, 2013; Fauré 2002; Bécaud 2006; Fig. 1), was originally recognized only from England and France (Buckman 1911 and Monestier 1931, respectively). Subsequently, several studies extended its paleogeographical distribution, but did not report stratigraphic occurrences outside the Bifrons Zone. Dagis (1968) and Wierzbowski *et al.* (1981) illustrated *Porpoceras* specimens from the Polare Zone in Siberia and Spitsbergen, respectively (correlating with the uppermost part of the NW European Bifrons Zone; Jakobs 1992: fig. 3-1); Hillebrandt & Schmidt-Effing (1981) and Hillebrandt (1987) reported *Porpoceras* specimens from the Pacificum Zone in South America (correlating with the NW European Bifrons Subzone; Rulleau *et al.* 2013: 104); and Jakobs (1997) described *Porpoceras* specimens from the Ionica Zone in western North America (correlating with the NW European Bifrons Zone; Jakobs 1992: fig. 3-1).

Noteworthy, although Rulleau *et al.* (2013: 101) stated that the genus *Porpoceras* occurs precisely in the Bifrons Horizon in the NW European realm (Fig. 1), same authors reported two quite unusual occurrences of *Porpoceras* in France: one specimen of *Porpoceras* sp. was found in the Semipolitum Horizon (Rulleau *et al.* 2013: 103, pl. 35, fig. 3) and another specimen of *Porpoceras* sp. was retrieved from the *Apertum* Horizon (Rulleau *et al.* 2013: pl. 30, fig. 3; see Fig. 1).

More importantly, three studies reported additional unusual stratigraphic occurrences for the genus *Porpoceras*. Guex (1973) described the oldest known occurrence of the genus (*Porpoceras gigas* Guex, 1973) based on a unique specimen from the Early Toarcian Falciferum Subzone in Morocco (Fig. 1). This important specimen extends back the stratigraphic range of *Porpoceras* and it is currently the only known occurrence reported from the Mediterranean realm. However, due to its poor preservation, the taxonomic assignment of this specimen to the genus *Porpoceras* remains doubtful. In addition, Rulleau *et al.* (2013) mentioned that Bécaud (unpublished data) found *Porpoceras* in the Lower Toarcian (Douvillei Horizon; Fig. 1) of Vendée (western France). Finally, Gabilly (1976) mentioned, but did not illustrate, the occurrence of *Porpoceras* sp. in the Variabilis Subzone (Fig. 1) in the Thouars area (western France). Due to the lack of figured material, Rulleau *et al.* (2013) considered as doubtful this youngest occurrence of *Porpoceras*.

Here, we describe and illustrate two specimens of *Porpoceras* gr. *vortex* (Simpson, 1855) *-verticosum* Buckman, 1914 from the Middle Toarcian Variabilis Subzone of the Airvault quarry (near Thouars, western France), thus confirming that the stratigraphic range of the genus should be extended beyond the Bifrons Horizon in NW Europe.

GEOLOGICAL SETTING

The two specimens were found in the Airvault quarry (western France; Fig. 2). During the Toarcian, this site belonged to the NW European realm (Bécaud 2006; Rulleau *et al.* 2015) and it is supposed to correspond to a shoal area (Gabilly 1976; Bécaud 2006; Fig. 2). In the Airvault quarry, the Middle Toarcian stratigraphic succession was exposed along trenches. However, the Early and Middle Toarcian beds in this quarry are now flooded and are thus no longer accessible.

The Middle Toarcian comprises three distinct beds (Fig. 3: Beds 3 to 5). Bed 3 is a 40 cm thick oolithic packstone to wackestone that represents the Sublevisoni Subzone (characteristic species found: e.g., *Hildoceras sublevisoni* Fucini, 1919; Fig. 4A). The presence of 15-20% ooids embedded in a micritic matrix, the fragmentation of the associated bioclasts and the presence of an erosion surface at the base of this bed argue for a deposition under storm-induced influences. Bioturbation is pervasive throughout the bed, obliterating almost

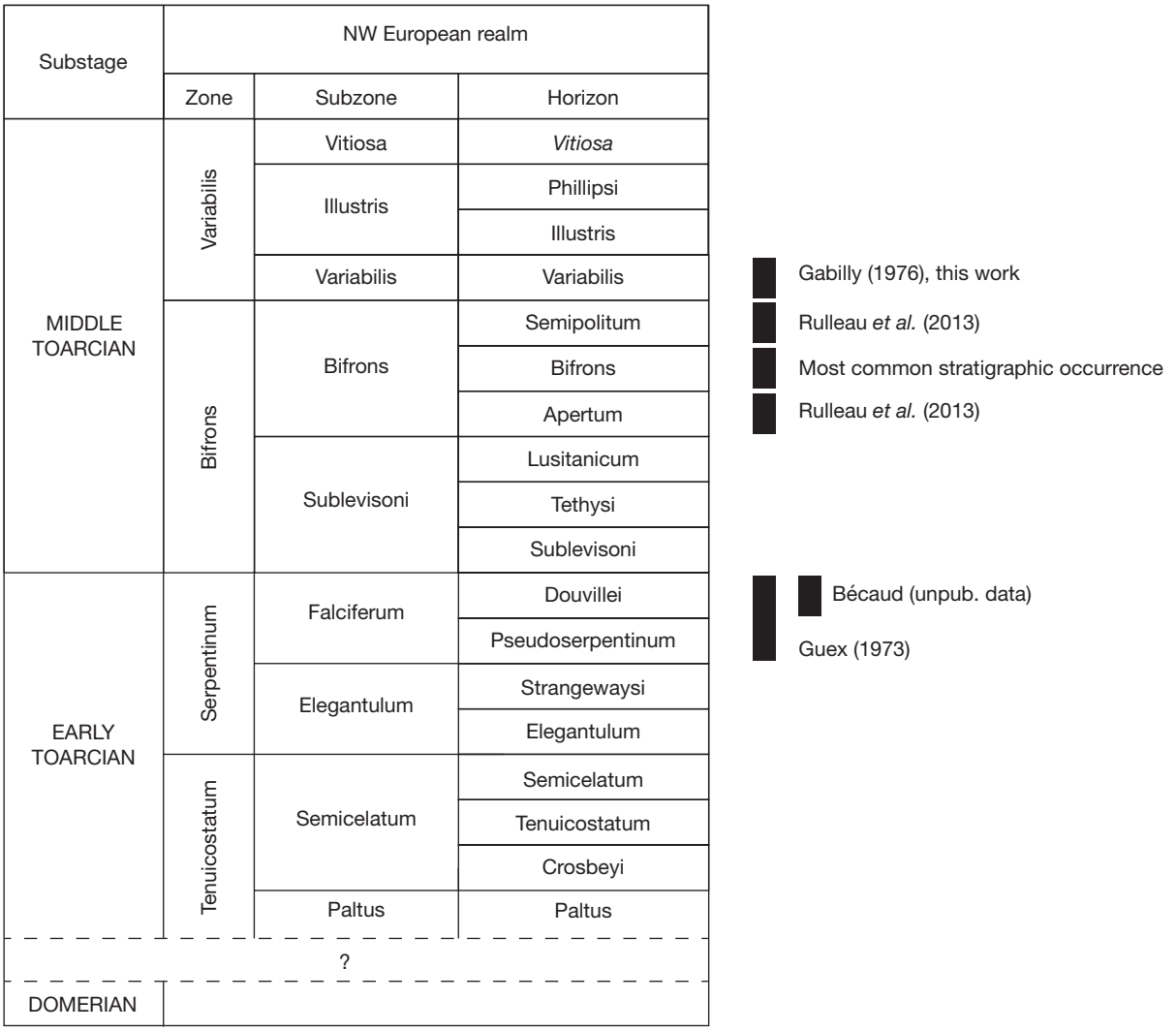

Fig. 1. — Early and Middle Toarcian ammonite biostratigraphy for the NW European realm, with stratigraphic occurrences of the genus *Porpoceras* Buckman, 1911 in the NW European realm and Morocco (Guex 1973). Modified after Rulleau *et al.* (2013).

all the original sedimentary structures. This bed was probably deposited in the uppermost offshore environment. Bed 4 (Fig. 3A) represents the Bifrons Horizon (characteristic species found: e.g., *Porpoceras* gr. *vortex-verticosum* and *Hildoceras bifrons* (Bruguière 1789; Fig. 4B-H and Fig. 4I, respectively) and is characterized by a 25 cm thick ochre limestone, whose sedimentological features are characterized by a low content of ooids (less than 5%), 20% of ferrugineous bioclasts, a high micritic matrix content (up to 40%) and high bioturbation intensity. Even though the bioturbation obliterates almost all the original structures, the low fragmentation of bioclasts, the presence of wavy laminations and the absence of sorting argue for an upper offshore environment affected by intermittent hydrodynamic episodes related to distal storm processes.

Bed 5 is a 60 cm thick grey limestone composed of an alternation of bioclastic-rich levels and mud-dominated intervals. The base of Bed 5 is affected by an erosion surface that is covered by a first 10 cm thick highly bioturbated bioclastic accumulation composed of echinoderms, bivalves and ammonites. The presence of reworked and fragmented echinoderms and bivalves embedded in a micritic matrix, together with complete ammonites, indicates local intermittent hydrodynamic episodes under storm influences. It passes vertically to low-energy conditions as indicated by: 1) a succession of a 20 cm thick mud-rich interval characterized by a low bioclastic content that includes ammonites; 2) a 20 cm thick bioaccumulation of ammonites and large bivalves (*Plagiostoma*) with disarticulated shells showing both convex-up and concave-up orientations; and 3) a 10 cm thick mud-rich interval with well-preserved complete ammonites. There is neither taphonomical nor sedimentological evidence for a mass-flow transport or the reworking of the material in Bed 5. The *Plagiostoma* accumulation cannot be interpreted as a storm-induced layer because there is no erosional base, ammonites are well-preserved, and the valves of *Plagiostoma* are complete and intensively encrusted by oysters, bryozoans and serpulids. This layer (Fig. 3B) corresponds to a typical condensed facies generated by a starvation in sediment. Overall, Bed 5 is considered as a low energy environment corresponding to an

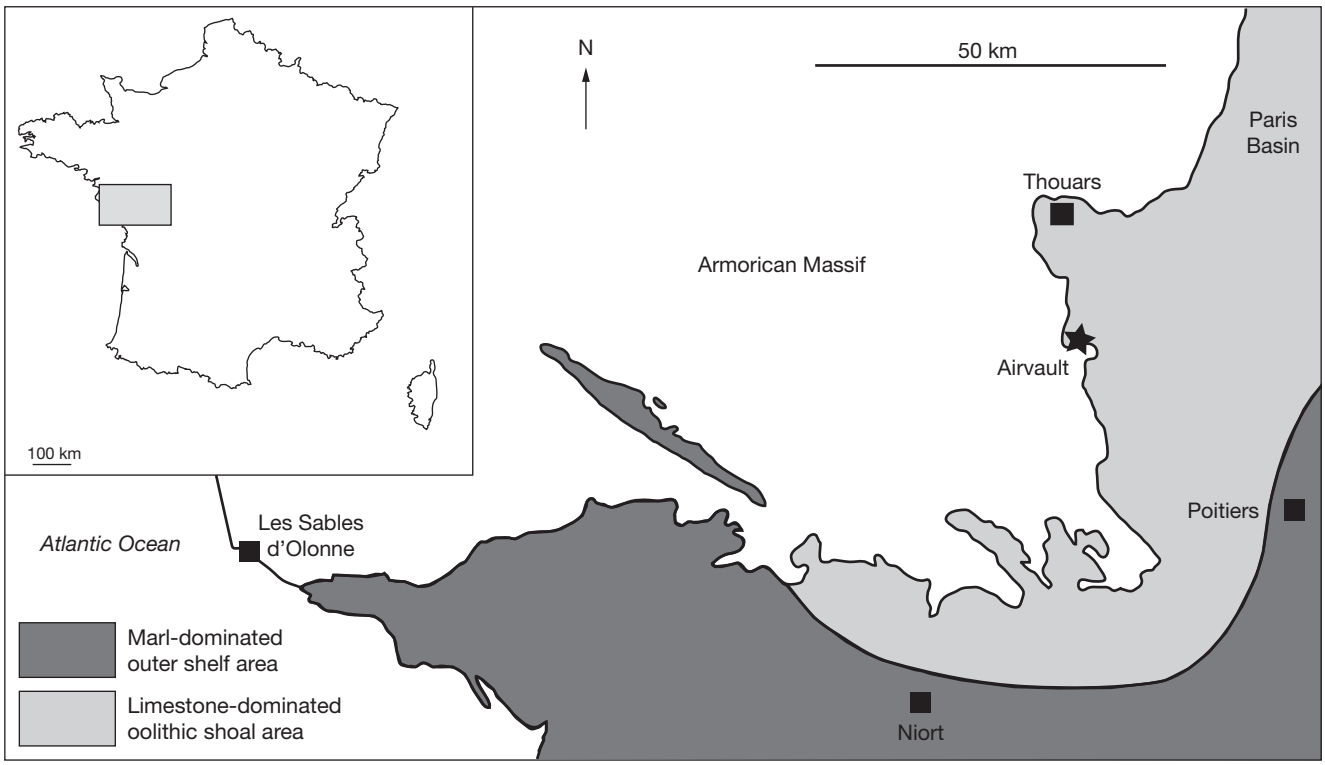

Fig. 2. — Simplified map of the Early and Middle Toarcian up to the Variabilis subzone in the Thouars area (Western France). Modified after Bécaud (2006).

upper to lower offshore with rare storm-induced processes at the base. Bed 5 includes the Semipolitum Horizon (uppermost part of the Bifrons Subzone, Fig. 1) and the Variabilis Subzone. We place the transition between the Semipolitum Horizon and the Variabilis Subzone at the beginning of the *Plagiostoma* bioaccumulation, based on the massive apparition of *Haugia variabilis* (d'Orbigny, 1844) specimens; even though the species *Hildoceras semipolitum* Buckman, 1902 rarely occurs within the Variabilis Subzone (Bécaud 2006; Lacroix 2011; this work). Associated ammonite fauna from the Variabilis Subzone in the Airvault quarry mainly includes *Haugia variabilis* (Fig. 4J), *H. jugosa* (Sowerby, 1815), *H. navis* (Dumortier, 1874), *Denckmannia tumefacta* Buckman, 1898, *D. malagma* (Dumortier, 1874), *D. rudis* (Simpson, 1843), *Pseudolioceras lythense* (Young & Bird, 1828), *Mucrodactylites mucronatus* (d'Orbigny, 1845), *C. raquinianum* (d'Orbigny, 1844) and *Catacoeloceras dumortieri* de Brun, 1932 (this work; see also Bécaud 2006 for a thorough list).

Overall, these sedimentological and palaeontological features are in agreement with the work of Gabilly *et al.* (1985) who interpreted the condensation of the Variabilis Subzone in the Airvault quarry as a first order sedimentation crisis initiated in the Semipolitum Horizon.

The two *Porpoceras* specimens described herein (Fig. 5A, B) were retrieved from the 10 thick mud-rich interval at the top of the condensed Variabilis Subzone, at the very top of Bed 5 (Fig. 3B). One additional specimen of *Porpoceras* from the Bifrons Horizon of the Belmont quarry (eastern France) is also figured for comparison (Fig. 5C).

Abbreviation

Repository of figured and measured specimens is abbreviated UBGD (Université de Bourgogne, Géologie Dijon).

SYSTEMATIC PALAEONTOLOGY

Family Dactylioceratidae Hyatt, 1867
emend. Buckman (1909)
Subfamily Dactylioceratinae Hyatt, 1867

Genus *Porpoceras* Buckman, 1911

Type species. — *Ammonites vortex* Simpson, 1855 by monotypy.

Porpoceras gr. ***vortex*** (Simpson, 1855)
-verticosum Buckman, 1914
(Figs 4B-H; 5)

Ammonites vortex Simpson, 1855: 60.

Porpoceras vortex – Buckman 1911: pl. 29A. — Géczy & Szente 2007: pl. 8, fig. 4.

Porpoceras verticosum Buckman, 1914: pl. 91.

Porpoceras gr. *vortex-verticosum* – Rulleau *et al.* 2013: 101, pl. 29, fig. 2; pl. 30, figs 1, 2; pl. 31, figs 1, 3, 5; pl. 32, figs 1, 3-6; pl. 33, figs 1, 2; pl. 34, fig. 1.

Porpoceras vortex – Kovàcs 2014: 50, pl. 2, figs 2, 7; pl. 4, fig. 5.

FIG. 3. — **A**, Stratigraphic succession of Middle Toarcian beds in the Airvault quarry; **B**, close-up view of the upper part of the Variabilis subzone in the Airvault quarry, with a *Porpoceras* specimen (UBGD 279076, see Fig. 5A) in situ indicated with a circle.

FIG. 4. — **A**, *Hildoceras sublevisoni* Fucini, 1919 (UBGD 279080, Sublevisoni Subzone, Airvault); **B**-**H**, *Porpoceras* gr. *vortex* (Simpson, 1855) -*verticosum* Buckman, 1914 (**B**-**E**, UBGD 279078, Bifrons Horizon, Airvault; **F**-**H**, UBGD 279079, Bifrons Horizon, Airvault); **I**, *Hildoceras bifrons* (Bruguière, 1789) (UBGD 279081), Bifrons Horizon, Airvault); **J**, *Haugia variabilis* (d'Orbigny, 1844) (UBGD 279082), Variabilis subzone, Airvault). Scale bars: 10 mm.

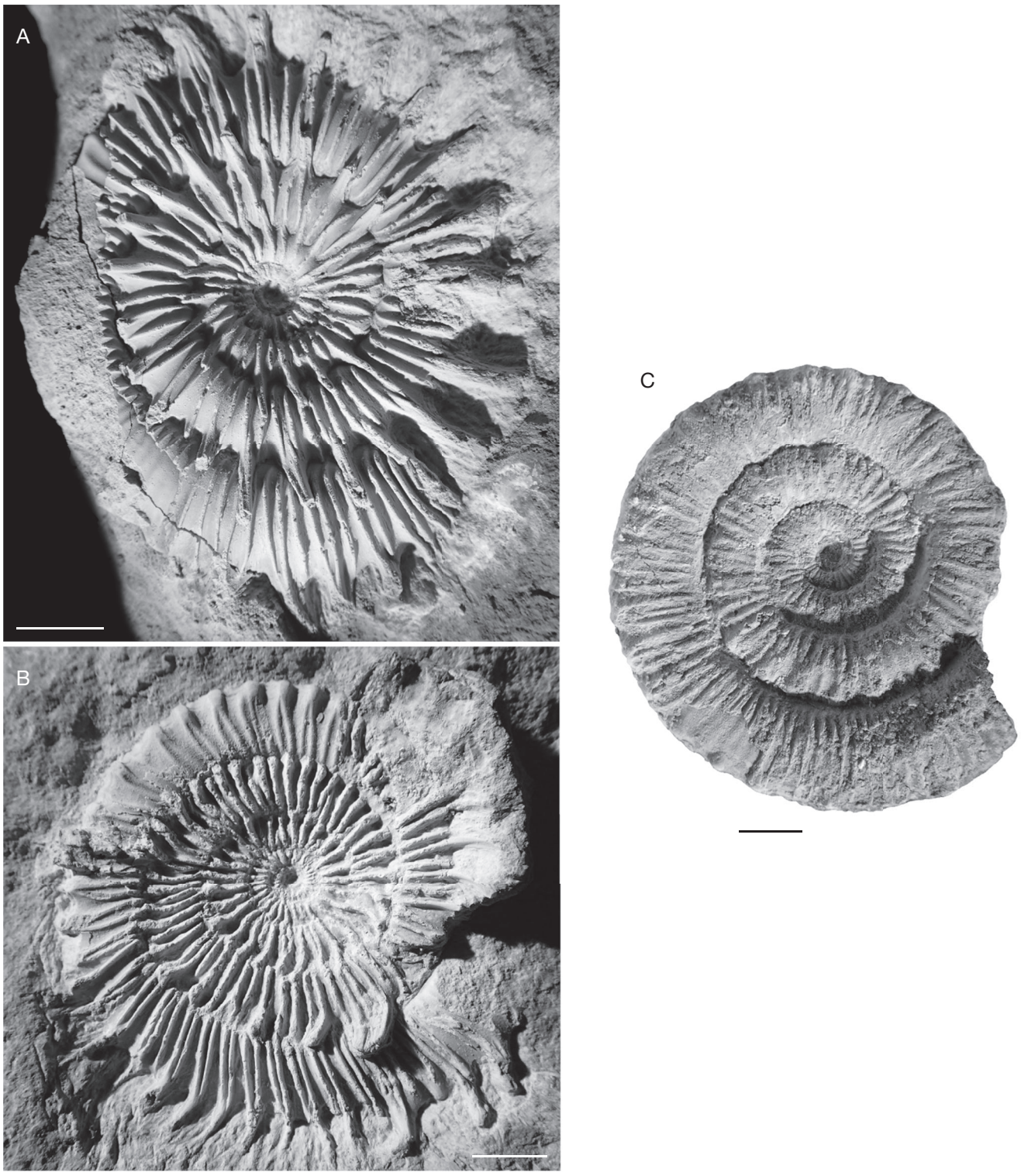

Fig. 5. — **A**, **B**, Specimens of *Porpoceras* gr. *vortex* (Simpson, 1855) -*verticosum* Buckman, 1914 from the Variabilis Subzone of the Airvault quarry; **A**, UBGD 279076; **B**, UBGD 279077; **C**, specimen UBGD 279075 of *Porpoceras* gr. *vortex-verticosum* from the Bifrons Horizon of the Belmont quarry. Scale bars: 10 mm.

Description

Very evolute shell with a cadicone whorl section on inner whorls, becoming quadratic to depressed on mature whorls. Every two, three or four primary ribs, one primary rib bears a ventro-lateral tubercle. Ribs are often grouped by two on the same tubercle. This ornamentation is constant throughout ontogeny. Each tubercle bears a very developed spine leaning on the following whorl and not visible on internal molds. Suture lines not visible on the specimens from the Airvault quarry.

TABLE 1. — Measurements (in mm) of *Porpoceras* gr. *vortex* (Simpson, 1855) -*verticosum* Buckman, 1914 specimens from Airvault quarry (UBGD 279076, UBGD 279077), from Belmont quarry (UBGD 279075), from Anduze, Gard (France, 1665 F-2) and of the holotypes of *Porpoceras vortex* (WM 153a) and *Porpoceras verticosum* (WM 220a) from Whitby, Yorkshire (England). Abbreviations: **D**, Diameter; **H**, whorl height; **W**, whorl width; **U**, umbilical diameter.

Genus	Species	Specimen	D	H	W	U	H/D	U/D	Remarks
Porpoceras	*vortex-verticosum*	UBGD 279076	59	13.3	–	34.8	0.23	0.59	–
Porpoceras	*vortex-verticosum*	UBGD 279077	57.3	11.5	–	35.2	0.20	0.61	–
Porpoceras	*vortex-verticosum*	UBGD 279075	74.7	18.7	–	43.5	0.25	0.58	–
Porpoceras	*vortex-verticosum*	1665 F-2; Rulleau *et al.* (2013: pl. 32, fig. 1)	78	17	20.5	47	0.22	0.60	–
Porpoceras	*vortex*	WM 153a; Buckman (1911: pl. 29A)	83	15	26	53	0.18	0.64	Holotype
Porpoceras	*verticosum*	WM 220a; Buckman (1914: pl. 91)	71	15	18.5	43	0.21	0.61	Holotype

MEASUREMENTS

See Table 1.

STRATIGRAPHIC AND PALAEOGEOGRAPHICAL OCCURRENCES

From the uppermost part of the Serpentinum Zone (?) to the Variabilis Subzone; found in NW Europe, Siberia, Spitsbergen, North and South America.

DISCUSSION

According to Rulleau *et al.* (2013), it is extremely difficult to distinguish *P. vortex* from *P. verticosum*, even with a large number of specimens. They therefore decided to include these two species within the same group and we concur with this taxonomic opinion. *Porpoceras* differs from *Catacoeloceras* and *Mucrodactylites* by its well-developed ventro-lateral tubercles and ribs generally grouped by two on the same tubercle. The resembling genus *Peronoceras* is older and does not exhibit tubercles on inner whorls (Rulleau *et al.* 2013).

DISCUSSION

STRATIGRAPHIC RANGE OF *PORPOCERAS* IN THE MEDITERRANEAN REALM, NORTH AND SOUTH AMERICA, SIBERIA AND SPITSBERGEN

The genus *Porpoceras* was found in North and South America, Siberia and Spitsbergen within zones equivalent to the NW European Bifrons Zone (see Introduction part).

In the Mediterranean realm, Guex (1973) reported the oldest known occurrence of the genus from the Falciferum Subzone (Early Toarcian) in Morocco, although based on a unique specimen with a doubtful generic assignment.

STRATIGRAPHIC RANGE OF *PORPOCERAS* IN NW EUROPE

The genus *Porpoceras* is usually regarded as an excellent marker of the Middle Toarcian Bifrons Horizon in the NW European realm (Rulleau *et al.* 2001; Fauré 2002; Bécaud 2006; Rulleau *et al.* 2013). However, such a biostratigraphic restriction is challenged by several reports. First, one specimen of *Porpoceras* sp. was found in the Semipolitum Horizon (Rulleau *et al.* 2013: 103, pl. 35, fig. 3) and another specimen of *Porpoceras* sp. was retrieved from the *Apertum* Horizon (Rulleau *et al.* 2013: pl. 30, fig. 3; Fig. 1). Second, Rulleau *et al.* (2013) mentioned that Bécaud (unpublished data) also found *Porpoceras* in the Lower Toarcian (Douvillei Horizon) of Vendée (western France). Third, the specimen of *Porpoceras* sp. reported by Gabilly (1976) from the Variabilis Subzone of the Thouars area was not figured and could not be retrieved, so that this youngest occurrence has remained uncertain so far. Finally, the material described and illustrated here (Fig. 5A, B) represents the youngest unambiguous occurrence of *Porpoceras*, in the Variabilis Subzone.

The absence of *Porpoceras* in the Variabilis Subzone of the coeval Belmont quarry in eastern France is surprising as Toarcian levels are well developed in this quarry and were extensively sampled and studied in the last two decades (Elmi & Rulleau 1991; Rulleau 1993a, b, 2001, 2006, 2009). It can thus be hypothesized that the genus went nearly extinct at the end of the Bifrons Horizon, but it survived up to the Variabilis Subzone in the Thouars area.

Based on its youngest occurrence reported in this work, we also hypothesize that *Porpoceras* went extinct in the Illustris Subzone, together with *Catacoeloceras* and *Mucrodactylites*, coinciding with the drastic loss of diversity observed between the Bifrons and Variabilis Zones in NW Europe, during the Bifrons-Variabilis extinction (Dera *et al.* 2010). Recognized by O'Dogherty *et al.* (2000) at the species scale, this extinction event is even more obvious at the genus level (Dera *et al.* 2010). High extinction rates associated with a drastic decline in origination rates during the Variabilis Zone seem to be to cause of the considerable drop in ammonite richness observed during this event (Dera *et al.* 2010).

CONCLUSION

This study provides the first robust evidence for the youngest occurrence of *Porpoceras* in the Variabilis Subzone. It confirms the previous mention of *Porpoceras* sp. by Gabilly (1976) in the Variabilis Subzone of western France. Consequently, the known stratigraphic range of *Porpoceras* now extends from the uppermost part of the Serpentinum Zone (taking into account the specimen reported by Guex 1973) to the Variabilis Subzone. Nevertheless, its occurrence outside the NW European Bifrons Horizon is extremely rare and *Porpoceras* remains an important, but not exclusive taxon to characterize this biostratigraphic unit.

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